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LIFE HISTORY OF THE THREESPINE STICKLEBACK *Gasterosteus aculeatus* Linnaeus IN KARLUK LAKE AND BARE LAKE KODIAK ISLAND, ALASKA

BY JOHN GREENBANK AND PHILIP R. NELSON

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ABSTRACT

The threespine stickleback occurs in large numbers in Karluk Lake, Kodiak Island, Alaska, an important water in studies of red salmon production. The life history of the stickleback in Karluk and Bare Lakes presents many interesting phases. It has few lateral plates, which is characteristic of the fresh-water sticklebacks. It has a lifespan of about two-and-one-quarter years and in that period spawns once, or twice at the most. Structurally, the stickleback is hermaphroditic. It feeds on planktonic invertebrates and insect larvae. A possible interrelationship between stickleback and juvenile red salmon is that both consume the same kinds of food. Both species are preyed on by the Arctic charr.

FE HISTORY OF THE THREESPINE STICKLEBACK *Gasterosteus aculeatus* nnaeus IN KARLUK LAKE AND BARE LAKE, KODIAK ISLAND, ALASKA

y John Greenbank[1] and Philip R. Nelson, *Fishery Research Biologists*, BUREAU OF COMMERCIAL FISHERIES

)ver a period of many years, investigations ve been made by the U. S. Fish and Wildlife vice at Karluk Lake and Bare Lake on diak Island, Alaska. These have covered, pri-ily, the production of red (sockeye) salmon. ey have embraced many biological and limno-ical factors which are related to salmon pro-tion, including the presence in these waters other fishes whose life histories are interre-d with that of the red salmon.

)ne of these species is the threespine stickle-k, *Gasterosteus aculeatus* Linnaeus, which oc-s in large numbers in these lakes. As a part the field studies, stickleback specimens were ected, seine hauls that captured sticklebacks e recorded, stomach samples were analyzed, samples for age determination were taken, numerous observations of habits were made. Most of the fieldwork on the sticklebacks was e by Nelson, and crews under his supervision. enbank has analyzed and evaluated the data. present this report as a summary of our wledge of the stickleback in these waters and relation to red salmon production, and as a tribution to the life history of the species.

. Y. Conkle, Robert F. Raleigh, C. S. Thomp-, Carl E. Abegglen, and others assisted in the ection of specimens and information. The wings were made by R. J. Kramer; the pho-raph for figure 13 was taken by Fred Rabe. ormation on the Karluk Lake sticklebacks was nished by C. E. Walker of the Fisheries Re-rch Institute.

HISTORY AND LITERATURE

he threespine stickleback is widespread and ly observed and has been studied by many kers through the centuries. A large number references exist in the published literature. Many of these, however, consist of little more than notes regarding such things as nest-building behavior.

Leiner (1929, 1930, and 1934) has studied the species intensively. Bertin (1925) published a monograph on sticklebacks. Many of his conclusions have been objected to by later workers, but at least he stimulated research and thought.

M. J. Heuts has made a thorough study of the threespine stickleback in Western Europe and has published (1947, 1947a, and 1949) important papers on variation, physiology, and genetics.

Wunder (1928, 1930) published the results of studies and experiments concerning behavior. The reproduction of the stickleback has been described by Craig-Bennett (1931) and others. Food studies have been made by Markley (1940) and by Hynes (1950). Age and growth of three species of sticklebacks in the British Isles have been worked out by Jones and Hynes (1950).

In North America, few papers have dealt at length with the life history of the stickleback. Cox (1922) reviewed the various species of sticklebacks of the Hudson Bay region; Myers (1930) made a study of races of the threespine stickleback in California and Lower California; and Vrat (1949) reported on the reproduction of the threespine stickleback in California.

DESCRIPTION OF THE WATERS

The southwestern section of Kodiak Island (fig. 1), in which Karluk Lake and Bare Lake lie, is a low plain with numerous mountains rising from it. The coastline is broken by many bays. The drainage pattern is involved. The vegetation is tundralike, composed of grasses, various flowering plants, willows, and alder, with cottonwood and birch trees irregularly distributed along the stream courses.

The area lies in a temperate climate, with much cloudy weather and a mean annual rainfall of about 50 inches. The air temperature ranges

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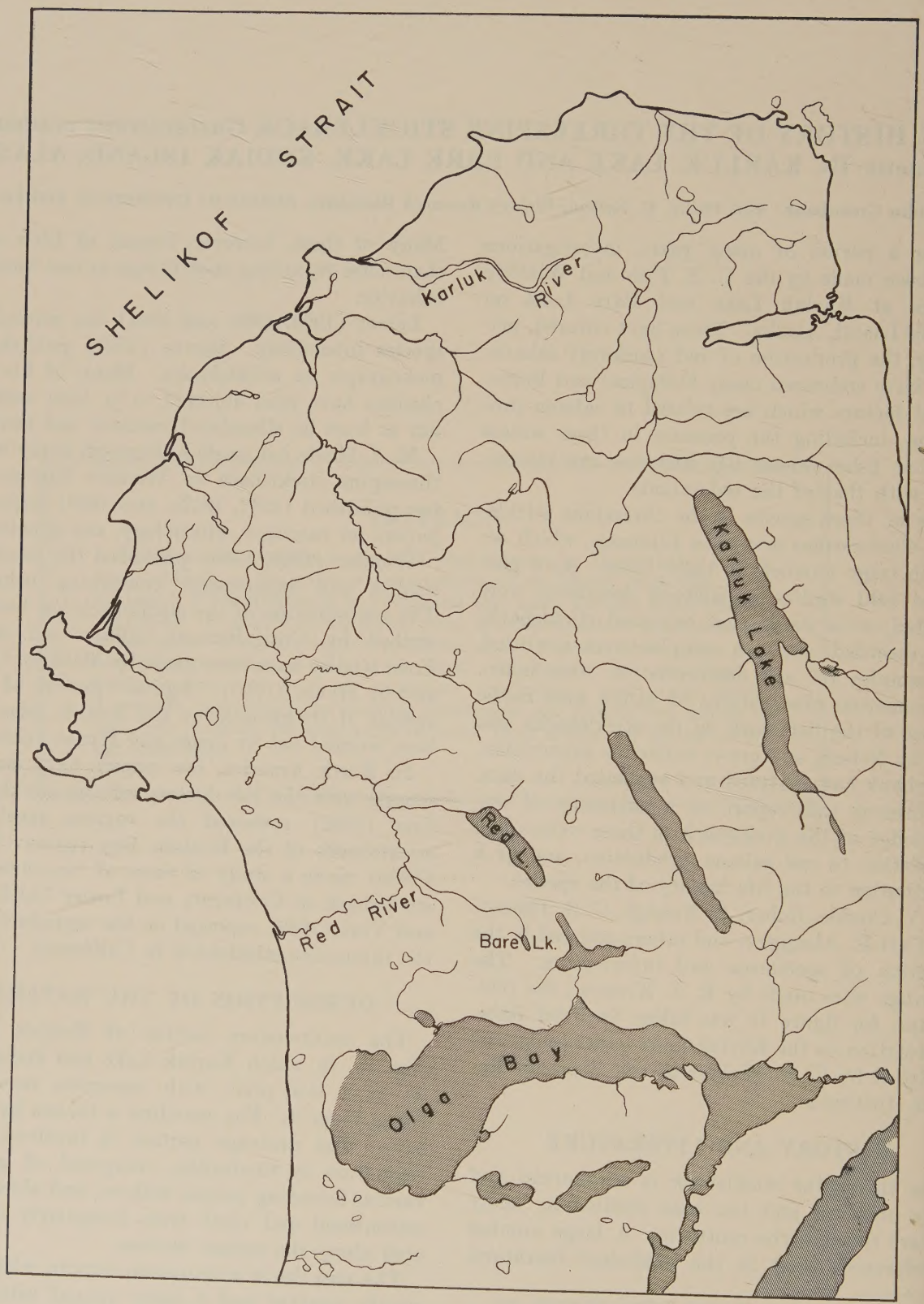


FIGURE 1.—Western Kodiak Island.

om below –18° C. in winter to above 29° C. summer.

Karluk Lake is drained by Karluk River, hich flows some 23 miles and empties into Kar-k Lagoon, and thence into the ocean. Several hall streams plus the drainage of two small kes, Thumb and O'Malley, flow into Karluk ake.

The physical and chemical characteristics of arluk Lake have been described by Juday et al. 932). The lake lies at an elevation of 350 feet ove sea level. It is 12 miles long; its greatest idth is 2 miles, and its area 15 square miles. has relatively little shoal area, only 10 percent the total area being less than 30 feet deep. he maximum depth is 410 feet. The beaches are gravel and rubble, the predominant rock mate-al being shale. The water is clear, has a pH nging from 7.0 to 8.7, and is low in carbonate d in total dissolved minerals. It contains an undance of dissolved oxygen at all depths roughout the summer.

Bare Lake is only 15 miles from Karluk Lake t belongs to another drainage. It is drained a small stream, Bare Creek, that flows into ed River.

Bare Lake is 380 feet above sea level. It is ghtly less than 1 mile long; its greatest width 1,600 feet, and its area about 120 acres. The aximum depth is 25 feet and the mean depth feet. The bottom is gravel and rubble on the oals and soft mud in the deeper area. The emical characteristics are similar to those of arluk Lake.

In both Karluk Lake and Bare Lake, vegeta-on is sparse. The predominant forms are water oss, *Fontinalis;* quillwort, *Isoëtes;* and water ttercup, *Ranunculus.* There are scattered tches of filamentous algae, and in Karluk Lake ere are beds of sparse *Potamogeton.*

Juday et al. (1932) have described the plankton Karluk Lake, and Nelson and Edmondson 955) that of Bare Lake. Bottom-dwelling ani-ls are few in numbers of species. Diptera rvae, especially of Chironomidae, are abundant places, and there are larvae of caddis flies richoptera), mayflies (Ephemeroptera), and her insects. Included also are pea clams (Pele-poda) and snails (Gastropoda).

The fishes of Bare Lake consist of seven species: red salmon (*Oncorhynchus nerka*), coho salmon (*Oncorhynchus kisutch*), and king salmon (*Oncorhynchus tshawytscha*); rainbow or steelhead trout (*Salmo gairdnerii*), Dolly Varden charr (*Salvelinus malma*), threespine stickleback (*Gasterosteus aculeatus*), and a fresh-water sculpin (*Cottus aleuticus*).

Karluk Lake has, in addition to these species, arctic charr (*Salvelinus alpinus*) and chum salmon (*Oncorhynchus keta*). Pink salmon (*Oncorhynchus gorbuscha*) spawn in Karluk River and a few enter the lake. Small numbers of the ninespine stickleback (*Pungitius pungitius*) have been seen in Karluk Lake (Charles E. Walker, private communication, 1956).

Karluk Lake has been the site of extensive biological investigations. These date back to 1889, when Tarleton H. Bean made a reconnaissance survey of the lake. Various scientists visited Karluk Lake in the years between 1900 and 1920. Henry O'Malley and Charles H. Gilbert made a survey of the salmon spawning grounds in 1921.

In 1926, a party led by Willis H. Rich conducted a limnological study of the lake including a physical survey (Juday et al., 1932). Studies of the lake, especially of its red salmon runs, have been carried out on a year-to-year basis since then.

A weir for counting adult red salmon ascending the Karluk River was installed near the mouth of the river in 1921. It was moved in 1942 about 13 miles upriver, and moved again in 1945 to its present location just below the outlet of Karluk Lake. The current investigations include counts and estimates of adult salmon entering the lake, of spawning salmon in the tributary streams, and of young salmon leaving the lake to go to the ocean. Studies also are being made of certain aspects of the life history of the red salmon and of the limnology of the lake.

Bare Lake was selected by the Fish and Wildlife Service (Nelson and Edmondson, 1955) for experiments in lake fertilization, because it represents the waters of the area and yet is small enough to be worked on feasibly. Preliminary surveys were conducted in 1949, and each summer, starting with 1950, the lake has been treated with commercial fertilizer. Various limnological

observations have been made as a means of assessing the effectiveness of fertilization in increasing lake productivity.

BIOLOGY OF THE STICKLEBACK

Since it was named and described by Linnaeus in 1758, *Gasterosteus aculeatus* has had a long and involved nomenclatural history. Specific and subspecific names have been based in the main on variations in the numbers of bony plates and of fin rays, on length of spines, and on selection of environment.

The threespine stickleback in Karluk and Bare Lakes is of the partially armored form. For present purposes, we shall not assign to it a name designating a subspecies or variety, but shall simply refer it to the species *Gasterosteus aculeatus*.

The ninespine stickleback, *Pungitius pungitius* (Linnaeus), is the only other member of the family which occurs in the waters of the North Pacific area, and it is found only in small numbers in Karluk Lake.

The sticklebacks as a group (family Gasterosteidae) differ considerably in morphology and appearance from even their nearest relatives among the fishes. They are small fish and have as a distinguishing character a number of isolated (free) stout spines in front of the dorsal fin. These spines are short but sharp pointed. At the posterior side of each spine is a small, triangular fin membrane. The dorsal spines can be erected or depressed by the fish and will lock weakly in the erect position. There is one short anal spine, and the pelvic fin consists of one heavy spine and one or two rudimentary rays. There are no scales, but some of the species ha bony plates.

Gasterosteus aculeatus, the threespine stick back, is a moderately slender, streamlined fish. T snout is somewhat pointed. The caudal pedun is slender, the tail shallowly forked (fork leng of fish equals approximately 0.97 times tot length). The anal fin originates well back the dorsal fin (almost even in *Pungitius pu gitius*). The species is extremely variable numbers of lateral bony plates and fin ra Figure 2 represents an adult threespine stick back from Karluk Lake.

The color varies with the locality and the ty of water. Except for spawning males, dull ton predominate. Generally the upper surfaces a olive, greenish, or brown, the colors becomi lighter on the sides. The ventral surface is lig yellow, white, or silver. Dark-brown pigment tion occurs in small indefinite blotches and in variable pattern of transverse patches along t sides. The fins are pale. The rays of the pe toral fin are outlined by lines of small dots black pigment. The breeding female in Karl and Bare Lakes does not assume any bright colo ation. The male, in breeding season, from t snout to the back of the pelvic fin, is red yellowish-salmon colored. The color tones a clear but not bold. Bluish tints may appe along the sides and on the face. Vrat (194 mentions the iridescent blue-green color in t iris of the eye of the breeding male and indicat that this color is noticeable for a period of ma days or weeks. We have found this condition hold for the Kodiak Island sticklebacks.

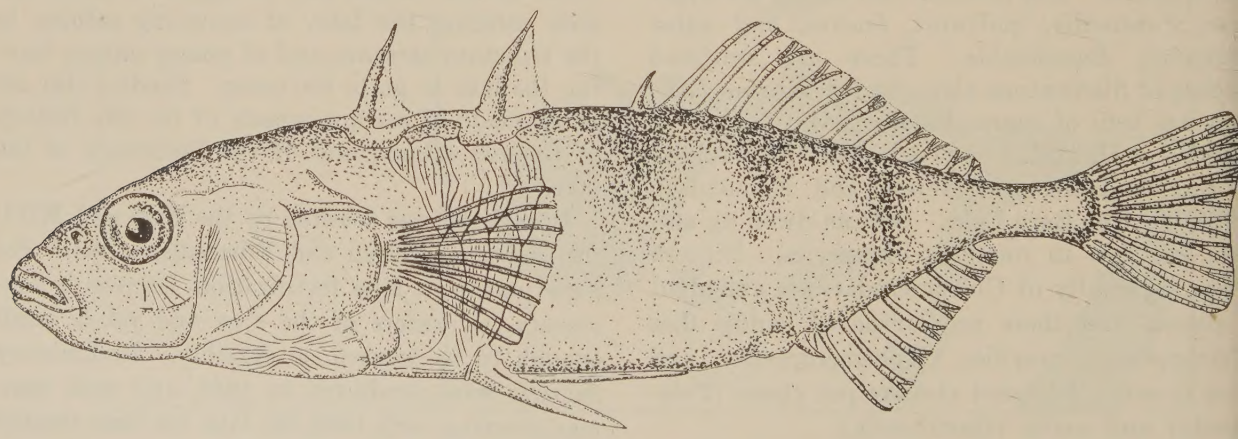


FIGURE 2.—Adult threespine stickleback (*Gasterosteus aculeatus*).

When the female is approaching the time of spawning, the belly becomes distended visibly. In the early part of the year, before the breeding characters are evident, the two sexes look much like.

Morphological Variation

Throughout its geographical range, the species *Gasterosteus aculeatus* is subject to a large amount of morphological variation. There are minor differences in color and color pattern and in body shape. More pronounced variations occur in numbers of vertebrae, fin rays, and lateral bony plates.

Within the species, the number of lateral plates varies from none to about 35. Most of the long list of specific, subspecific, and racial names which have been used have to do with the degree of armature.

It has long been recognized that populations which are year-round inhabitants of fresh waters have few plates, while those that live in salt water, and enter fresh water only for spawning, are many-plated. Bertin (1925) made an analytical study of populations of threespine stickleback throughout Europe and came to the conclusion that the number of bony plates is directly correlated with the salinity of the environment, and that a continuous gradation occurs from water of high salinity to fresh water.

However, Heuts (1947, 1947a) presents strong evidence that such a clinal gradation does not exist. The European stickleback populations are, instead, of two types, one of which shows a strong mode at about 5 to 7 plates, the other having a mode at around 32 plates. Within a given population, individuals with an intermediate number of plates may occur, but there are no populations which consist only or largely of fish with intermediate plate numbers. Therefore, Heuts concludes that individuals with an intermediate number indicate only a skewed distribution curve of one type or the other and not a genotypical intermediacy.

On the Atlantic coast of North America, both the form with many plates and that with few are present (Bigelow and Schroeder, 1953). As in Europe, the fish with strong armature are to be found in salt water, while the fresh-water populations generally have few plates. The same situation occurs also along the Pacific coast of North America.

The geographic pattern of variability in Alaskan waters has not been worked out thoroughly. Marine collections have been few, and in many fresh waters the species has been recorded without reference to which of the two forms was present. It is likely that there are many bodies of fresh water, particularly those close to the sea, in which both the many-plated and the partially plated forms may occur, at least for part of the year. An instance is Chignik Lake on the south side of the Alaska Peninsula (private communication from Fredrik Thorsteinson of the Fisheries Research Institute, 1956).

There is very little, if any, migration of the Karluk and Bare Lakes sticklebacks to and from the ocean. No substantial numbers of sticklebacks have been observed in movement in Bare Creek or upper Karluk River. There is no evidence of a sea-run stock of sticklebacks in either lake. The number of lateral plates on all specimens examined does not exceed nine.

Plates and fin rays were counted on a total of 200 fish from each of the 2 lakes. The total for each lake was made up of 4 subsamples of 50 fish each, taken in different years (table 1).

Each subsample probably included individuals of at least 2 age groups; therefore, there is considerable overlapping of year classes. However, as there is little if any exchange of stock with outside populations, the genetic makeup of the population of the lake should be about the same from one year to the next.

TABLE 1.—*Subsamples of fish taken in different years from Karluk and Bare Lakes*

Karluk Lake	Subsample *a*	1956
	b	1949
	c	1949
	d	1948
Bare Lake	Subsample *w*	1956
	x	1954
	y	1950
	z	1951

An additional sample consisted of 50 specimens from O'Malley River, a tributary to Karluk Lake. This sample was taken in 1951.

The lateral plates were counted on the left side of the fish under low-power magnification. The point of a scalpel was used to lift the edge of each plate, so that none would be missed in counting. The first (most anterior) plate is

small and sometimes hard to find. Fin rays were counted in the dorsal and anal fins and both pectoral fins. In counting the (soft) rays, each element was counted as one ray. The last (most posterior) two elements in the dorsal and anal fins are well separated at the visible base of the fin, not jointed or branched as in some groups of fishes, and hence were counted as separate rays.

Numbers of lateral plates are shown in table 2. The Karluk Lake fish have from 5 to 9 plates, with no specimen having 4. The mean for 200 specimens is 6.55. The fish from Bare Lake have from 4 to 7 plates, no individuals having 8 or 9. The mean for 200 specimens is 5.22.

Between the various pairs of subsamples from Karluk Lake, there are significant differences (for the most widely separated pair, subsamples *c* and *d*, $t=8.0$ and $P<0.001$). The subsamples were captured at different places on a large lake and probably represent separate subpopulations.

TABLE 2.—*Number of lateral plates on stickleback from Karluk and Bare Lakes*

Subsample	Number of plates						Mean	σ	σ_M
	4	5	6	7	8	9			
Karluk Lake:									
Subsample *c*	----	1	12	31	6	----	6.84	0.64	0.09
a	----	----	18	26	4	2	6.80	.75	.11
b	----	2	25	15	4	4	6.66	.97	.14
d	----	10	35	5	----	----	5.90	.54	.08
Total	----	13	90	77	14	6	6.55	.84	.06
O'Malley River	----	5	26	14	5	----	6.38	0.80	0.11
Bare Lake:									
Subsample *w*	6	19	21	4	----	----	5.46	.81	.12
x	8	24	18	----	----	----	5.20	.69	.10
y	6	29	14	1	----	----	5.20	.66	.09
z	13	22	15	----	----	----	5.04	.75	.11
Total	33	94	68	5	----	----	5.22	.74	.05

The means for the samples of 200 fish each from the 2 lakes differ by 1.33. The difference is highly significant ($t=16.8$; $P<0.001$).

For the sample from O'Malley River, the mean number of lateral plates lies between the extremes for Karluk Lake.

The number of dorsal spines has a high degree of constancy. Of 400 specimens from the 2 lakes, 391 had 3 spines, only 9 (2.2 percent) had 4 spines, and none had 5 or 2. The fourth spine, when present, may be small and near the last spine, or it may be almost as long as the middle spine and be inserted midway between the last 2 of the 3 normal spines (fig. 3). The fourth

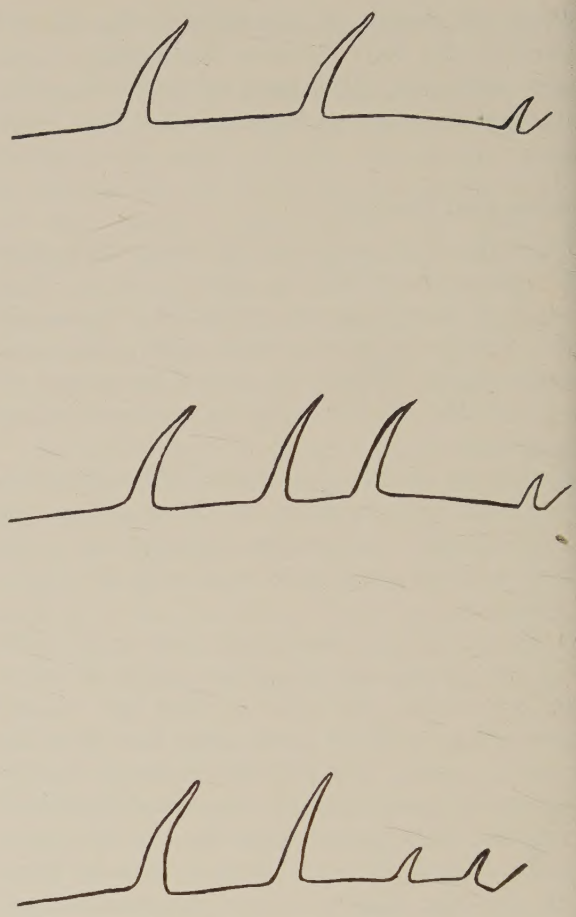


FIGURE 3.—Insertion of dorsal spines. Top, normal position of 3 spines. Center, fourth spine about the same size as, and inserted just posterior to, the second spine. Bottom, fourth spine small and inserted just anterior to third spine.

spine was not found to occupy a position anterior to the first normal spine or between the first two.

Counts of rays of the dorsal, anal, and pectoral fins are summarized in tables 3–5. In the numbers of dorsal and anal fin rays, there are differences, of varying degrees of significance, between the means of various subsamples from a given lake. These differences, however, definitely are overshadowed by the differences between the means of Karluk Lake and Bare Lake. In each of the latter instances, there is almost one fin ray difference, the mean number for Bare Lake being lower than that for Karluk Lake. The mean for the O'Malley River sample falls between the means for Karluk and Bare Lakes, for dorsal and for anal rays.

ABLE 3.—*Number of dorsal fin rays on sticklebacks from Karluk and Bare Lakes*

Subsample	Number of rays							Mean	σ	σ_M
	8	9	10	11	12	13	14			
rluk Lake:										
Subsample *c*			3	20	23	3	1	11.58	0.77	0.11
a			3	26	19	2		11.40	.66	.09
d			6	25	16	3		11.32	.76	.11
b			6	29	13	2		11.22	.70	.10
Total			18	100	71	10	1	11.38	.74	.05
O'Malley River		3	11	19	16	1		11.02	0.93	0.13
re Lake:										
Subsample *x*		3	27	18	2			10.38	.66	.09
w		6	22	21	1			10.34	.71	.10
y		3	30	16	1			10.30	.61	.09
z	1	2	28	16	3			10.36	.74	.10
Total	1	14	107	71	7			10.34	.68	.05

ABLE 4.—*Number of anal fin rays on sticklebacks from Karluk and Bare Lakes*

Subsample	Number of rays					Mean	σ	σ_M
	6	7	8	9	10			
arluk Lake:								
Subsample *c*		3	26	19	2	8.40	0.66	0.09
a	1	5	27	15	2	8.24	.76	.11
b		4	34	11	1	8.18	.59	.08
d		9	32	9		8.00	.60	.08
Total	1	21	119	54	5	8.20	.67	.05
O'Malley River	1	5	33	11		8.08	0.63	0.09
are Lake:								
Subsample *z*	2	25	20	3		7.48	.67	.09
w	2	25	22	1		7.44	.61	.09
x	3	31	16			7.26	.56	.08
y	3	34	12	1		7.22	.57	.08
Total	10	115	70	5		7.35	.62	.04

ABLE 5.—*Number of pectoral fin rays on sticklebacks from Karluk and Bare Lakes*

Location	Number of rays			Mean
	9	10	11	
arluk Lake	12	374	14	10.00
are Lake	6	378	16	10.02

The ranges of the counts differ also. For dorsal rays (table 3), the fish in Karluk Lake range from 10 to 14 with no individuals having 8 or 9. The Bare Lake counts range from 8 to 12, and no individuals have 13 or 14. For anal rays (table 4), the ranges are 6 to 10, and 6 to 9, for Karluk Lake and Bare Lake, respectively.

Heuts (1949) shows, for *Gasterosteus aculeatus* in Europe, a negative correlation between the number of dorsal and anal rays and the water temperature during development of the embryo. The water temperatures at the time of embryological development, in Karluk and Bare Lakes, are not known with any degree of accuracy.

For the sample from both lakes, there is a significant positive correlation between the number of dorsal rays and the number of anal rays in an individual fish. The figures for Karluk Lake are $r=0.46$, $P<0.005$; for Bare Lake, $r=0.22$, $P<0.005$.

The number of pectoral fin rays is remarkably constant (table 5). Of 800 fins counted (both fins of each of 400 fish), only 48 (6.0 percent) had more or fewer than 10 rays. The data are too few to yield information on correlation between numbers in the left and right pectoral fins.

Numbers

Almost every published account of the threespine stickleback in any location describes it in such terms as abundant, plentiful, or numerous. Low egg counts per female, and the fact that it spawns only once or, at the most, twice during its life, are balanced by a high rate of survival of young and the adaptability of the species to various physical conditions and types of food.

No quantitative estimates of stickleback populations have been made for Karluk and Bare Lakes. During three summers, a considerable number of fish marked by fin clipping were released in Bare Lake, but recoveries were inadequate to produce a reliable estimate of population numbers. Nelson and Edmondson (1955) state that the stickleback is the most abundant fish species in Bare Lake, and it may be so in Karluk Lake. Morton,[2] on the basis of fyke net catches, believed the stickleback outnumbered by far the juvenile red and coho salmon in the littoral zone in Karluk Lake.

Over almost any shoal of either lake, on almost any day in summer, sticklebacks may be seen in widely varying numbers. Usually they are more or less evenly distributed over a considerable area and are not in tightly packed clumps or streams. A single haul with a 70-foot beach seine, sweeping some 200 square yards, often catches from 300 to 1,500 sticklebacks. Large concentrations have been observed at the mouths of tributaries

[2] The ecology of two Alaskan charrs as shown by their parasites. By William Markham Morton. Master's thesis, University of Washington, Seattle. Typewritten, 31 pp., 1942.

to Karluk Lake, presumably fish in spawning migration.

The degree of fluctuation of numbers from year to year is not known. Certain beach locations in Bare Lake were seined several times each summer in the years 1951–55. The catches varied widely, from less than 50 to more than 4,000 (table 6). No attempt has been made to make a statistical analysis of the variance or to arrive at a measure of its significance; since many external factors, such as light and wave action, are involved. Assuming that these factors averaged out to some extent, there is indication that a population peak was reached in 1953.

The proportionate strength of the different year classes cannot be estimated, since seine hauls may not constitute random samples of the population.

TABLE 6.—*Seine hauls, southwest corner Bare Lake, and catch of sticklebacks per haul*

Date	Catch [1]	Average for year	Date	Catch [1]	Average for year
1951			*1955*		
July 8	1,000				
July 22	350	500	May 23	1,300	
Aug. 25	400		June 7	400	
Sept. 12	150		June 24	600	
			July 12	700	
1952			July 18	250	500
			July 30		
June 25	1,000		Aug. 10		
July 8	100	300	Aug. 17	100	
July 29	50		Aug. 27	150	
Sept. 11	50		Sept. 6	1,300	
1953			*1956*		
May 23	150		May 30	250	
June 8	1,700		June 20	500	
June 27	4,300	1,300	July 10	400	300
July 24	1,400		July 23	250	
Aug. 12	250		Aug. 4	200	
Aug. 26	150		Aug. 28	150	
1954					
May 23	850				
June 7	950				
June 24	300				
June 26	800				
July 12	650				
July 26	50	450			
July 29	[2]				
Aug. 7					
Aug. 10	700				
Aug. 17					
Aug. 27	250				
Sept. 28	250				

[1] Figures rounded to nearest 50.
[2] Dash indicates fewer than 25.

Habitat

Essentially, the stickleback in Bare and Karluk Lakes is an inhabitant of the shallow waters. A few fish, but no large numbers, have been observed on the surface of Karluk Lake at a considerable distance from the shore. Morto caught 12 sticklebacks in one set of a fyke n at a depth of 80 feet in Karluk Lake, but did n take any sticklebacks in a set at 200 feet. Sim larly, C. E. Walker (private communication) r ports having taken sticklebacks in Karluk Lal in a fyke net set at a depth of 30 feet but n in a net set at 126 feet.

Presumably, food is more readily obtainab along the shoals; although plankton animal which comprise a substantial part of the stickl back diet, are plentiful in at least the upp layers of the water in the center of the lak It is probable, also, that conditions of light, ten perature, and shelter are not as suitable to th stickleback in the lower levels as in the surfa water. Bigelow and Schroeder (1953, p. 309 state that *Gasterosteus aculeatus* in the Nort Atlantic Ocean often is picked up far from lan but nearly always on the surface, usually i patches of weeds.

There is little aquatic vegetation on the shoa of Karluk and Bare Lakes. Often, when di turbed, the sticklebacks dart to the bottom t hide among rocks and moss. Much of the tim they stay in open water and depend for prote tion on their appearance and behavior. Weed where present, furnish feeding opportunity i the way of insect larvae and small Crustac and Mollusca attached to the plants.

Age, Size, and Growth

In the published literature to date, the mo comprehensive work on age determination sticklebacks, which has come to our attention, that of Jones and Hynes (1950). These autho determined age by means of the otoliths and dre up growth-rate tables and curves for three sp cies of sticklebacks from the Birket River England.

We have examined otoliths of about 250 stickl backs from Bare Lake and Karluk Lake. Als we have drawn up length-frequency histogran for about 65 samples as described below. Th information obtained by the two methods is good agreement and provides a reasonably re able estimate of age and growth.

In preparing and examining the stickleba otoliths, we have followed essentially the tec nique used by Jones and Hynes. Only fresh fis

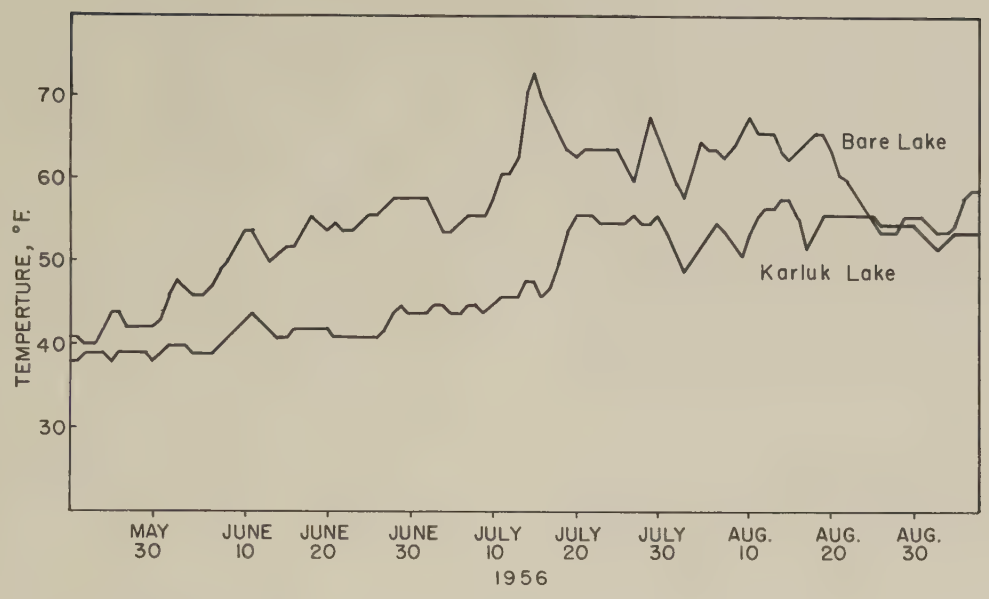


FIGURE 4.—Water temperatures, surface, summer of 1956. Upper curve, Bare Lake. Lower curve, Karluk Lake. Curves smoothed slightly.

r those preserved in alcohol, can be used, as ormalin destroys the otoliths in only a few veeks.

The standard length in millimeters, and the ex and state of maturity are recorded for each ish. Then, working under a low-power micro-cope, the top of the skull is sliced off, and the toliths are extracted by sharp-pointed forceps. Only the sagitta, the largest of the three otoliths o be found in each side of the skull, is used. Both sagittae from one fish are treated and mounted together.

The otoliths (sagittae) are placed in 65 per-ent alcohol, where they are cleaned of bits of issue. Then they are put into pure creosote for rom 5 to 15 minutes for clearing. Finally, they re mounted in Canada balsam or some other lear mounting fluid. They are read under a magnification of about 40 diameters, using a trong light reflected from the surface of the otolith, with a black mat background.

For a description of the appearance of the otolith and an interpretation of its markings, we quote Jones and Hynes.

The sagitta first appears when the fish is about 6 mm. ong, i. e., a few days after its emergence from the nest; he otolith is then a small body either uniformly trans-arent or more or less opaque. By the end of June the enter is usually completely formed. Otoliths in this tate or in an earlier state of development were desig-nated S—. During June or early July the first transparent (S) ring appears, followed by the opaque zone (+) which is visible in some fish in July and in all by September. At first the opaque zone is narrow, but it rapidly increases in width during the summer. From September until the following June the otoliths of all fish in their first year read S+, i. e., they consist of center, one transparent ring and an opaque zone. Thereafter the S ring becomes evident in July, not June or July as in young fish: This may be due to the fact that it is not so easy to see the S ring on the edge of the larger otoliths. The opaque zone (+) begins to be visible in August or September, and is present in all fish by October.

This delineation appears to hold true for the Kodiak Island sticklebacks with minor variations. In the otoliths from the Bare Lake and Karluk Lake fish, the transparent rings apparently form during a rather short period in June and early July. In about early August, the material which gives cloudiness starts to be deposited, Seemingly (although it is difficult to be certain), this material accumulates to some extent in the outer portion of the previously clear zone, as well as in a newly formed zone. Thus the result is that the apparent clear bands are narrower than the cloudy bands.

At any rate, in age determination each opaque ring (outside of the centrum and first transparent ring) is read as one winter (although the opaque band actually starts to form in late summer or early fall). For example, the otolith of a fish

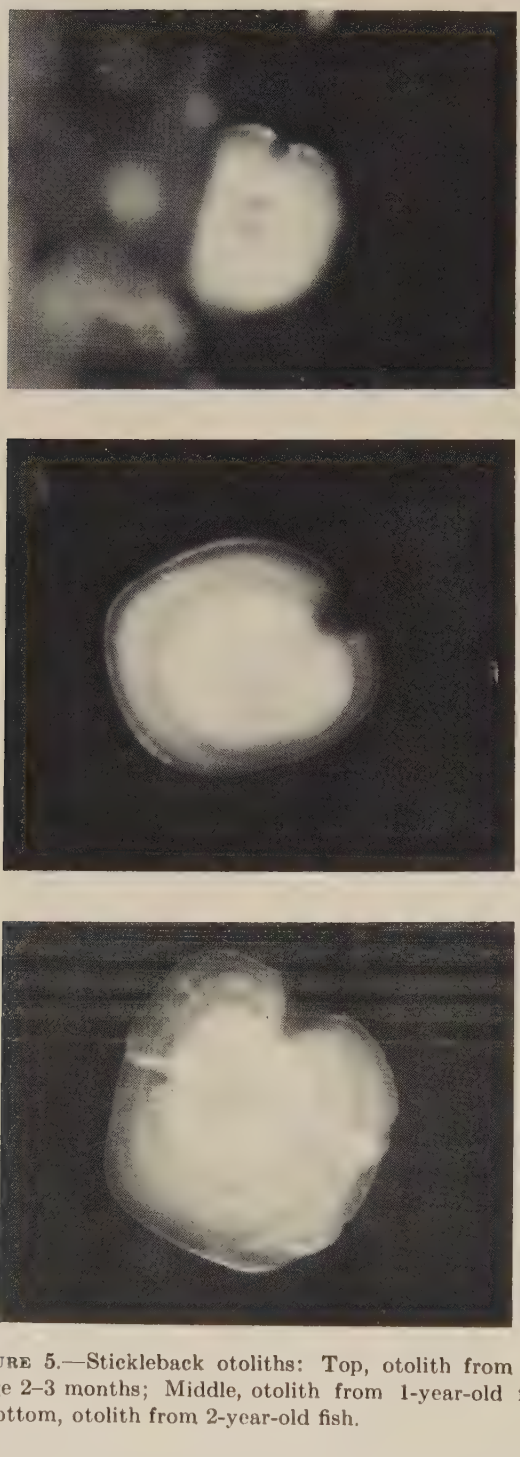


FIGURE 5.—Stickleback otoliths: Top, otolith from fish age 2–3 months; Middle, otolith from 1-year-old fish; Bottom, otolith from 2-year-old fish.

1 year old, taken in June, would show in order: centrum, first transparent ring, first opaque ring, and, at the outer edge, the beginning of the second transparent ring. The same fish, if captured in September of the same year, would have two transparent rings, and the second opaqu ring would be forming at the edge. Shown i figure 5 are photographs of otoliths taken fro fish of a few months, 1 year, and 2 years of ag

As mentioned by Jones and Hynes, the tim of formation of the light and dark rings in th otolith are not the same for all species of fis In certain fishes, such as *Clupea harengus*, th transparent ring appears to be formed in wint and the opaque ring in the summer, the rever of *Gasterosteus*.

Our samples for length-frequency determina tion were taken by seining, which is probabl more nearly nonselective as to size than any othe method available to us. However, it may be tha a completely random sample of the populatio cannot be obtained, since the sticklebacks ma sort and distribute themselves by size to som extent. It is believed though that size selectivit in the sampling is more or less smoothed out b the large number of samplings.

Samples in Bare Lake were taken at interva of 1 to 2 weeks during the summers (approx mately June 1 to September 1) of 1950–56, in clusive, and in Karluk Lake during the summe of 1948 and 1949. In Bare Lake almost all o the sampling was done in one area, the beach a the southwest corner of the lake. In Karlu Lake most of the samples were taken around o near Camp Island on the east side of the lak

Each sample consisted of from 100 to 400 fis Standard length of each fish was measured i millimeters. A length-frequency histogram wa drawn for each sample expressed in percentag of the total number of fish in the sample. Fo the Bare Lake samples, the lengths were groupe in 2-mm. intervals; for the samples from Karlu Lake, in 3-mm. intervals. The histograms show ing the sequence of samples from Bare Lake fo one summer (1954) are presented in figure 6. I figure 7 the sequence for Karluk Lake in th summer of 1949 is shown.

Standard lengths may be converted to for lengths or total lengths (all of these terms ar well defined in recent literature) by use of th following factors: F. L./S. L.=1.17, and T. L. S. L.=1.21.

Jones and Hynes (op. cit.) give a summary o the information regarding age and size of th threespine stickleback. Various authors hav

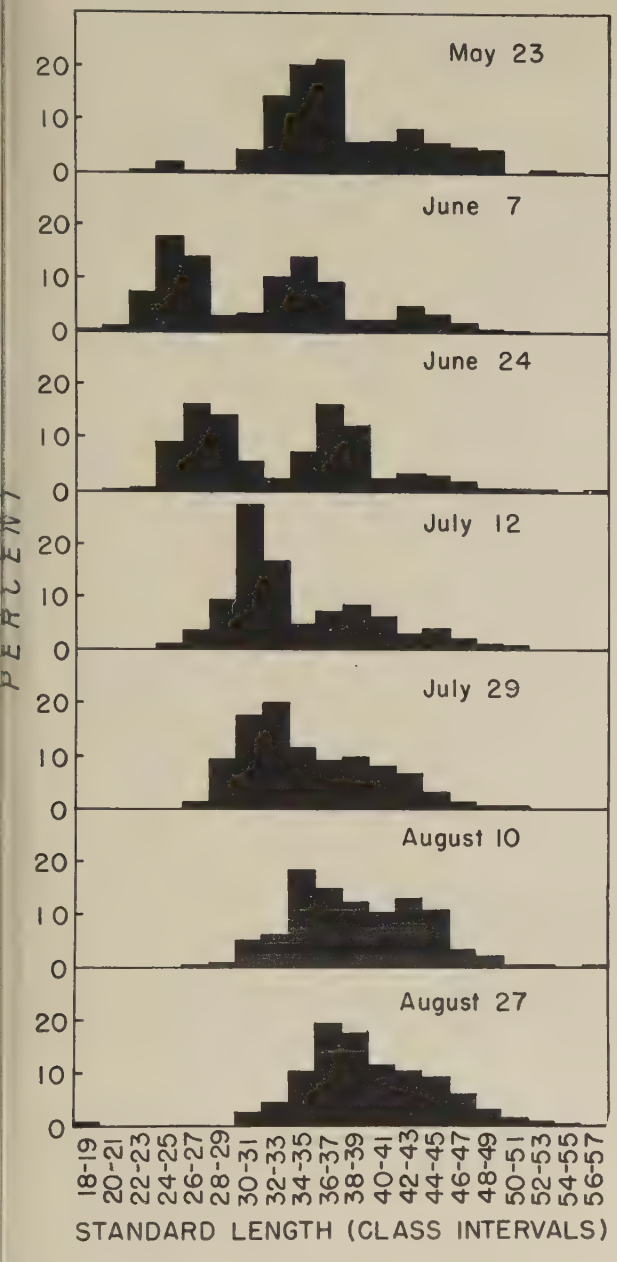


FIGURE 6.—Length-frequency histograms, sticklebacks from Bare Lake, 1954. Each diagram represents a sampling of 100–400 fish on a given date. Vertical ordinate, percent of total sample. Horizontal ordinate, standard length group.

placed the lifespan of the species at from 1 to 4 years. Some have said that the fish breeds only once, others that it may breed in each of 2 or 3 successive years. No doubt there is considerable variation, which is due to differences in race or strain or to environmental differences.

In the Birket River sticklebacks (*Gasterosteus aculeatus*), Jones and Hynes found the maximum lifespan to be 3 years plus. The fish at the end of the first summer of life (i. e., when a few months old) averaged about 24 mm., standard length. At the end of the second summer, the average was about 34 mm., and at the end of the third summer about 40 mm. Most of the growth occurred during the summer. Maximum size achieved was about 65 mm.

Assuming that our interpretation of the otoliths is correct, the sticklebacks in Karluk and Bare Lakes have a lifespan of about two and one-fourth years. Most of the 2-year-old fish die shortly after spawning, as indicated by the successively smaller numbers of large fish in the samples as the summer progresses. A very few otoliths appeared to show an extra winter ring. It may be that an occasional fish survives the third winter.

In the samples from Bare Lake in the summer of 1954 (fig. 6), at the time of the first sampling on May 23, very few young-of-the-year fish were present. The frequency mode at about 35 mm. apparently represented 1-year-old fish, the 2-year-old fish being much fewer and showing a broad frequency mode at about 45 mm.

In the next sample, taken on June 7, the small fish predominate, with a mode at about 25 mm. The fish of the other two size groups (age classes) have fallen off in comparative numbers. Successive samples throughout the remainder of the summer show: (1) a fairly rapid increase in size of the fish of the year; (2) a somewhat slower but steady growth of the 1-year-old and 2-year-old fish; and (3) a reduction in numbers of the older fish, especially of the 2-year-old group, probably caused by their death and disappearance from the population.

The same picture holds good for the summers of 1951 and 1953, with certain variations, probably caused in part by differences in spawning dates and hence in the growth achieved in the first summer. In the 1953 samples the 1-year-old group appeared in weak numbers throughout the summer, possibly indicating poor survival through the preceding winter.

In Karluk Lake in 1949 (fig. 7), the first sample of the summer was taken on June 23. The young-of-the-year group was almost or entirely

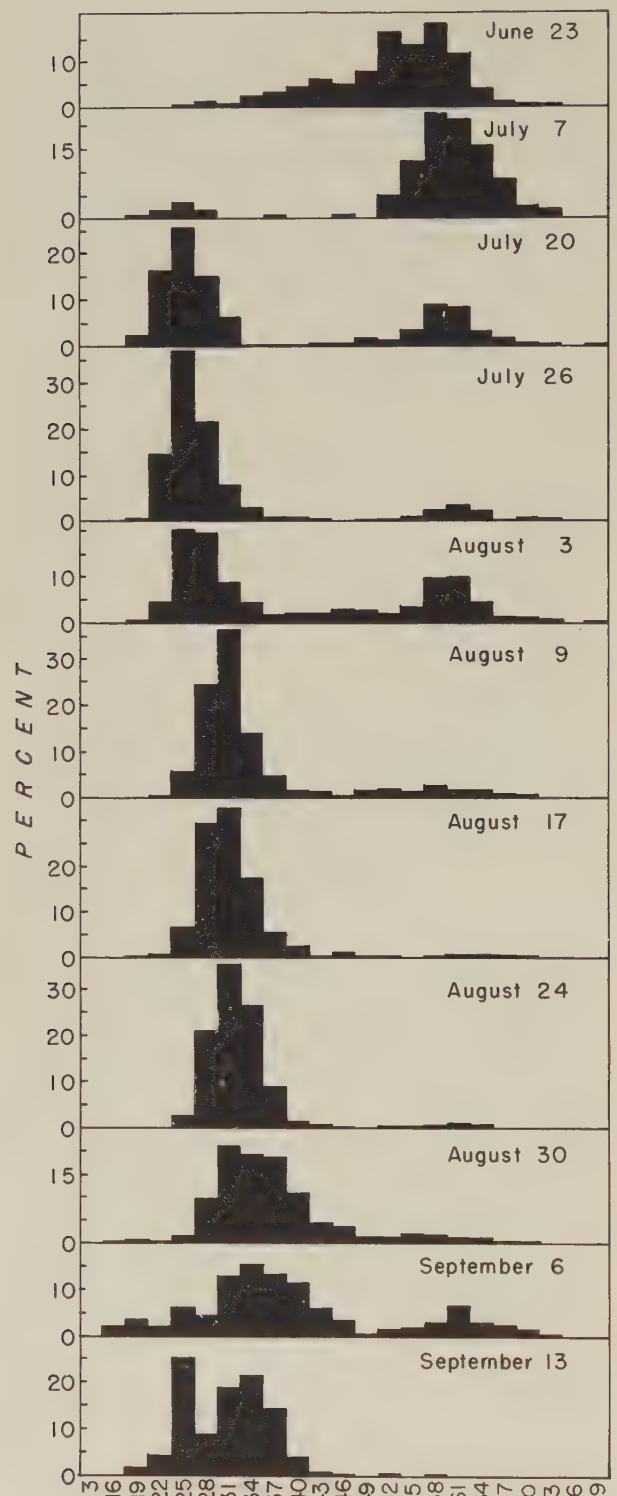


FIGURE 7.—Length-frequency histograms, sticklebacks from Karluk Lake, 1949. Arrangement as in figure 6.

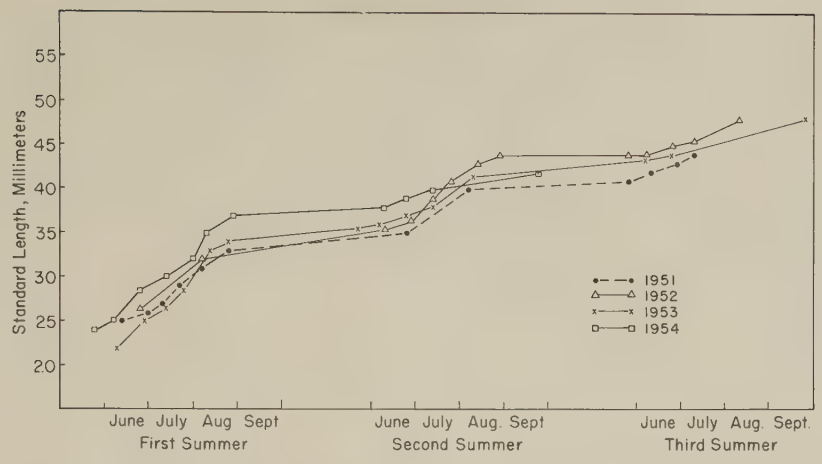
absent. It is thus indicated that the stickleback probably spawn later in Karluk Lake than i Bare Lake, presumably because the water warm up later in Karluk Lake. The next sample, take on July 7, contained a few small fish, and b July 20, the young fish predominated in number From that date through the remainder of th summer, the young-of-the-year were the grou with by far the largest numbers in the sample The older fish steadily dwindled in numbers, ex cept for a showing such as that on September possibly occasioned by nonrandom sampling. Ap parently, as in Bare Lake in 1953, the Karlu Lake stickleback population in the summer o 1949 was weak in 1-year-old fish; although, be cause of overlapping in size, some of the appar ent modes may have been composed of fish fror two age groups.

The Karluk Lake samples for September 6 an September 13, 1949, show an apparent bimodalit for the young-of-the-year group, probably cause by the appearance of a late hatched brood.

The figures in table 7 represent peaks (appar ent modes) in the length-frequency histogram for the sampling dates for Bare Lake. Eac vertical column thus portrays the growth of certain year class (fish hatched in the summe of a certain year), assuming that the peaks repre sent the average length of the fish of a particu lar age group at a given time.

These data are plotted in figure 8 as points o growth curves. Each curve in this figure repre sents the growth of the fish of a given year class The early growth, in the first few weeks afte hatching, cannot be shown, as the fish were no available in the areas sampled. Spawning n doubt takes place at different times in differen years, and the young fish thus get a slower o faster start and achieve a different average lengt at the end of the first summer. Thus in 1954 th hatching probably was early, and the first sum mer's growth was greater than in most othe years. Carrying over this increased growth, th fish of this year class were somewhat larger tha normal at the start of the next summer.

The growth curves for the year classes of 1951 1952, and 1953 fall close together (fig. 8). curve representing the average or composite fo these 3-year classes is redrawn in figure 9. Super imposed on it are symbols, each of which repre



IGURE 8.—Growth of Bare Lake sticklebacks. Each curve represents a year class. Points on curves derived from modes of length-frequency histograms.

ents a fish whose age was determined by otolith eading.

In these symbols, the sexes are separated for he fish in their third summer (2 years old). The females attain a somewhat larger size than ne males.

The fact that the curve, which presumably indicates average sizes, does not pass through the nedian of the lengths indicated by the otolith eadings may be due to an unconscious tendency n the part of the technician to select usually the rger fish in a given size-group for otolith amples.

In a similar diagram for the Karluk Lake ticklebacks (fig. 10), the symbols represent mean lengths of fish of length-frequency modes (for samples through the summers of 1948 and 1949), and the curve indicates the regression line as drawn by visual inspection. The vertical bars show the ranges of lengths of fish the ages of which were determined by otolith reading. Samples for otolith determinations were available only for dates in mid-July (1956).

As shown in figures 8–10, the Karluk Lake and Bare Lake sticklebacks do most of their growing from June 1 to September 1 and make comparatively little growth through the fall, winter, and spring.

The sticklebacks in Bare Lake average from 32 to 35 mm. in standard length at the end of

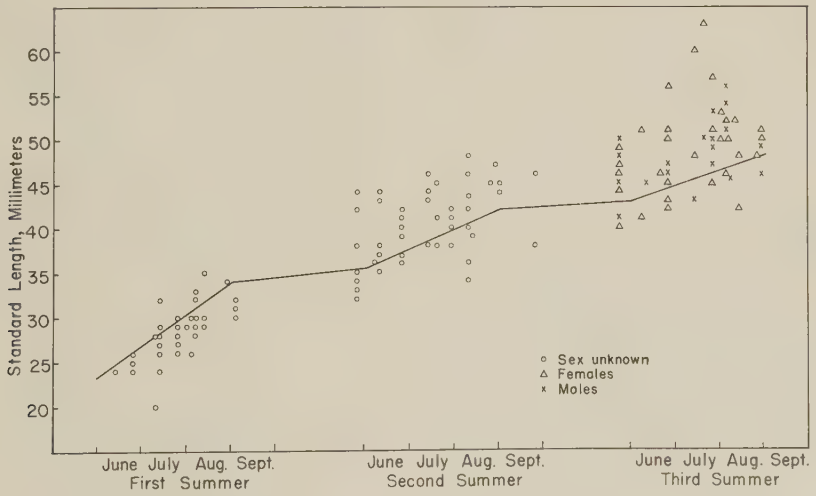


FIGURE 9.—Growth of Bare Lake sticklebacks. Curve is composite of growth of 3-year classes (from figure 8). Scattered points represent ages and lengths of individual fish determined by otolith reading.

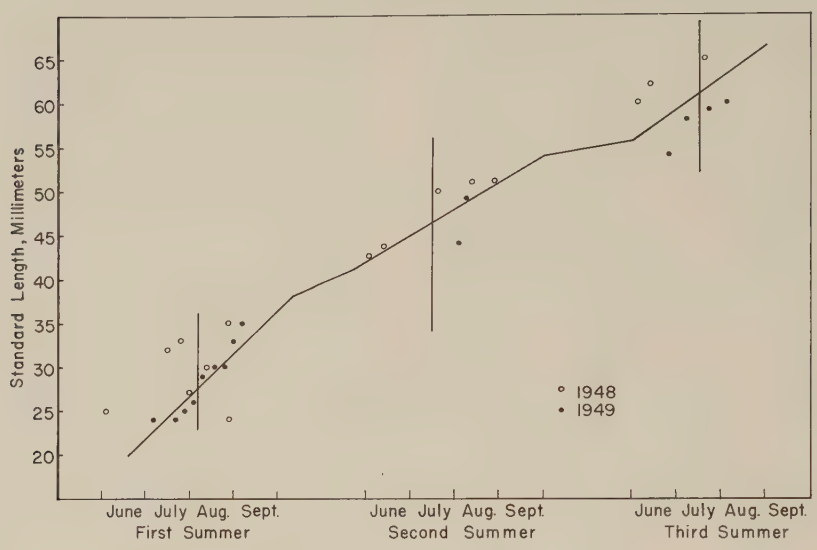


FIGURE 10.—Growth of Karluk Lake sticklebacks. Scattered points, modes from length-frequency histograms, 1948 and 1949. Curve drawn by inspection. Vertical bars, range of lengths from otolith readings.

TABLE 7.—*Bare Lake, average standard length of sticklebacks on various dates*

[Each entry in table represents a peak [mode] on length-frequency diagram of a sample taken on that date]

Sampling date		Year class					
Year	Date	1954	1953	1952	1951	1950	1949
1951	June 13				24	34	40
	June 29				25	35	41
	July 8				27	36	41
	July 22				30	39	44
	Aug. 7				31	39	
	Aug. 25				33	41	
	Sept. 12					42	
1952	June 25			26	35	41	
	Aug. 6			32	40	45	
1953	May 23				42		
	June 8		22	35	41		
	June 27		25	36	43		
	July 11		28	39	44		
	July 24		29	41			
	Aug. 12		34	43			
	Aug. 26		34	44			
1954	May 23	24	35	42			
	June 7	25	35	43			
	June 24	27	36	43			
	July 12	30	38	45			
	July 29	32					
	Aug. 10	35	43	48			
	Aug. 27	37					
1955	June 7	38	44				
	June 24	39	45				
	July 12	40	44				
	July 18	40					
	Sept. 25	42	48				

the first summer, depending somewhat on the date of hatching. At the end of the second summer (about 16 months after hatching), the average length is about 42 to 44 mm. At the start of the third summer, the average is about the same, and at the end of August of that summer, the few fish of that age group still alive are from 45 to 60 mm. long. The largest individual stickleback measured from Bare Lake was 69 mm. standard length (3.3 inches total length).

In Karluk Lake growth in the early part of the first summer is somewhat less than in Bare Lake because of later hatching. However, the growth thereafter is faster in Karluk Lake, and the maximum size achieved is greater. At the end of the first summer, the average standard length of the Karluk Lake fish is about 32 mm. At the end of the second summer it is about 50 mm. At the end of August in the third summer, the average for the fish of that age group still alive is about 60 to 65 mm. The maximum size recorded for Karluk Lake is 78 mm. standard length (3.8 inches total length).

The growth rate of the Karluk Lake and Bare Lake sticklebacks is greater than that of those in Birket River (Jones and Hynes, 1950), but the latter attain about the same maximum size, since they live 1 year longer. Sticklebacks of various populations from salt and fresh waters in western Europe (Heuts 1947a) ran up to 70 mm. standard length in maximum size.

Reproduction

The stickleback in Karluk and Bare Lakes spawns at the age of 1 or 2 years. It is strongly indicated that those fish of either sex which spawn at the age of 2 years die within a few weeks after spawning. In the late summer many

awned sticklebacks are found along the shores the lakes or at the outlets. These fish are her dead or in a weak, emaciated condition.

The proportion of sticklebacks that spawn at e 1 year is not known with certainty. Judging om egg development in females (ages obtained reading otoliths of 1-year-olds), fewer than e-half spawn at 1-year-old. Moreover, it is not own whether a stickleback that spawns at 1 ar dies, or lives another year without spawning ain, or spawns again the next year.

Bertin (1925) believed that the life cycle of e stickleback in Europe is accomplished in 1 ar (in other words, that the fish spawn at the e of 1 year), and that the fish die after breed-g. He stated, however, that in some localities e fish may live longer. Leiner (1934) wrote at *Gasterosteus aculeatus* breeds at least 2 or times during its life. Jones and Hynes (1950) und the sticklebacks in England to live 3 years d to show gonad maturation from the first ar, but did not indicate how many times the h spawns during its life.

The sexually mature sticklebacks are struc-rally hermaphroditic. Schneider (1904) re-rted an instance of hermaphroditism in *Gas-rosteus* in which one of the paired gonads ntained both ovarian and testicular tissue. W. Huver in 1955 discovered that the stickle-cks at Bare Lake and Karluk Lake have gonads both sexes present in the same fish, and Green-nk in 1956 examined a large number of mature ecimens and found all of them to show this ndition. In the ripe male (fig. 11), the testes e enlarged to occupy at least one-third of the dominal cavity. Between the testes and the ier organs, there is a thin septum. Against e ventral side of this septum lie the paired aries. These are 8 to 12 mm. long. They con-n no cells which can be identified under low-wer magnification as ova. No staining or tioning has been done.

The oviduct is Y-shaped and apparently enters e cloaca separately from the vas deferens. The aca is simple and is continuous with the hind t. There is a single external opening.

Just anterior to the cloaca and ventral or ghtly lateral to the posterior portion of the t, there is a pear-shaped, thin-walled sac some 8 to 12 mm. long. This sac, as spawning time approaches, becomes filled with a clear, viscous fluid, presumably the material which is used to cement the nest.

The ovaries of the ripe female (fig. 12) occupy a large proportion of the abdominal space. There is a septum as in the male. The testes are not prominent but definitely are discernible as rib-bonlike structures and readily distinguishable from the darker streak of the kidney. No cyto-logical examination of the testes has been made. The vas deferens and the oviduct apparently enter the cloaca separately as in the male.

A female stickleback, 70 mm. standard length, captured in Karluk Lake on July 25, 1956, had ovaries well distended with eggs. Among the eggs were several which were well eyed (fig. 13). While it may be possible that sperm cells had entered the cloaca from the water outside and had made their way up the oviduct, there is the possibility that the spermatozoa were derived from testicular material in the same fish.

Aside from the change in coloring in the male discussed earlier, and a visible swelling of the ripe female, secondary sex characters attendant on maturity are lacking.

There is little agreement in the literature about the time of spawning of *Gasterosteus aculeatus* or external factors with which it may be related. Roule (1945) states that the stickleback spawns in the latter part of spring or the first part of summer. Carl (1953) says that the spawning period is prolonged from the first week in April to the first week in September. In the estuaries and streams tributary to the Gulf of Main (Bige-low and Schroeder, 1953), the fish is said to spawn probably in May to June.

Eechhoudt (1947) was able to induce a con-siderable degree of sexual development in the stickleback by exposure to artificial light. Ap-parently this development did not reach the point of actual spawning.

We do not have information to fix the spawn-ing date of the sticklebacks in Karluk and Bare Lakes with any degree of precision. In Karluk Lake in 1948 stickleback eggs were recovered from a stickleback stomach on June 7. On the other hand, females still carrying ripe eggs were taken from Karluk Lake as late in the summer

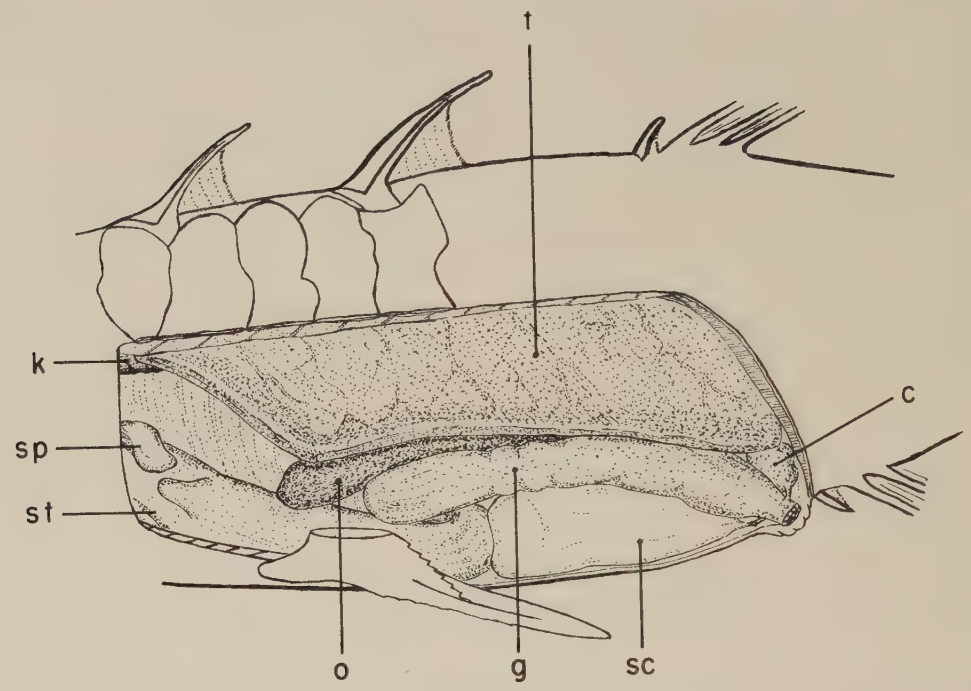


FIGURE 11.—Internal anatomy of normal, sexually mature, male stickleback showing presence of ovaries. c=cloaca g=gut; k=kidney; o=ovary; sc=sac; sp=spleen; st=stomach; t=testis.

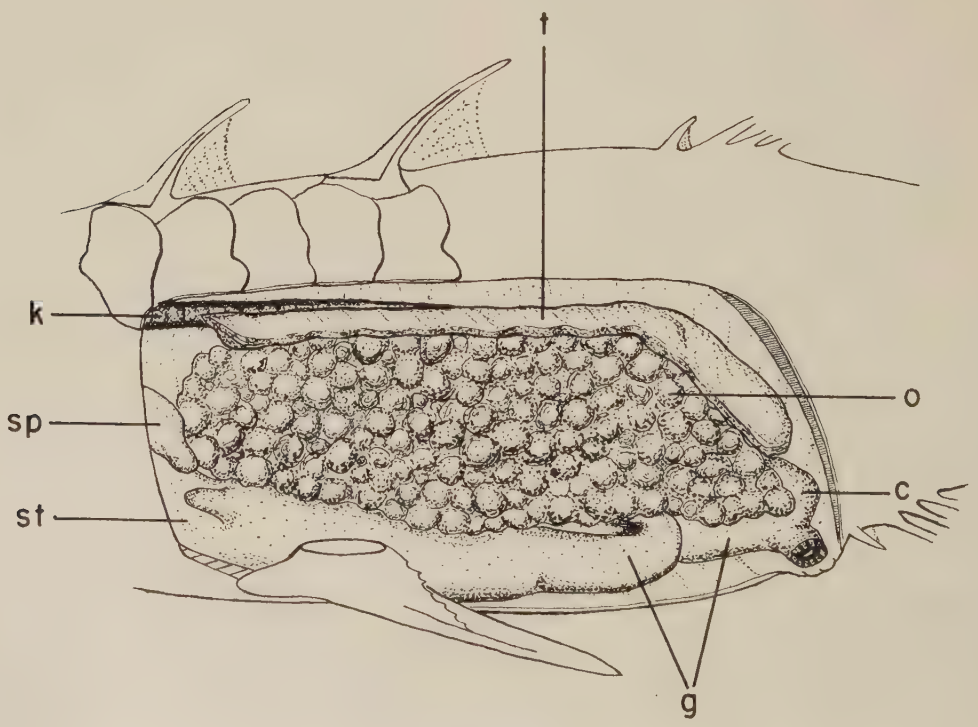


FIGURE 12.—Internal anatomy of normal, ripe, female stickleback showing presence of testes. c=cloaca; g=gut k=kidney; o=ovary; sp=spleen; st=stomach; t=testis.

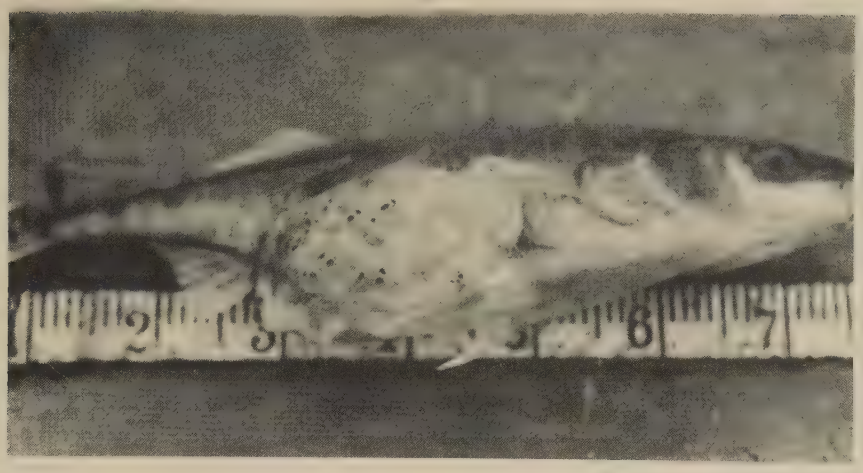


FIGURE 13.—Dissection of female stickleback with eyed eggs in ovary.

of 1949] as August 3. Morton[3] found stickleack eggs in the stomachs of charrs taken in Karlk Lake in June, July, and August, but not in ose taken in April, May, and September.

A collection of sticklebacks, made along the ore of Karluk Lake on July 15, 1956, had a w spawned-out females, but most of the females ere ripe with eggs. Observations on July 25 owed many females still to be carrying eggs. ut a collection made on August 6 had no fish ith ripe eggs, all the large females having awned.

In Bare Lake we have taken ripe females as rly as May 23 [1954] and as late as July 29 952]. Specimens less than 20 mm. standard ngth were captured on June 7, 1954. Judging om the size of the young-of-the-year in June d July (fig. 6), many of the sticklebacks in are Lake presumably spawn in May.

A collection from Bare Lake on July 23, 1956, d a few fish still gravid with eggs, but most of e mature fish were spent. On August 1 all the rger fish in a collection were spawned out. A st with eyed eggs in it was found on August 4, d on August 15 a young stickleback was taken. These scanty data indicate that perhaps the ckleback spawns earlier in Bare Lake than in arluk Lake. Such should not be the case if ght (length of day) were the sole factor controlling spawning date. Bare Lake, being small and shallow, warms faster in the early summer and maintains a higher surface water temperature through the summer than does Karluk Lake (fig. 4). It is suggested that water temperature may influence the time of spawning.

Spawning takes place in Bare Lake in shoal water around the shores of the lake. In Karluk Lake, too, many sticklebacks utilize the lake shore for spawning. Congregations of possibly hundreds of thousands of sticklebacks have been noted by C. E. Walker at the lower ends of Lower Thumb and O'Malley Rivers, the two principal tributaries of Karluk Lake, from early May until June 1950. Walker states (private communication) that the fish ascended these streams to Thumb and O'Malley Lakes, where they spawned.

The literature contains many references to the nest-building habits of the stickleback. In some waters the male constructs an elaborate nest of small sticks, twigs, or pieces of vegetation held together by a sticky substance presumably secreted by the kidney (Wunder 1930; and others). However, Vrat (1949) reports that the sticklebacks which he studied in California did not use leaves or twigs in their nests. These nests took the form of a hole in the sand, excavated by the male and shaped by strokes of his head.

The nests in Karluk and Bare Lakes are well hidden and camouflaged. The very few that we have been able to discover did not contain sticks or plant material but appeared to be made mostly

[3] Food studies of the Dolly Varden (*Salvelinus malma*) and tic charr (*Salvelinus alpinus*) at Karluk, Alaska, from 1939 ough 1941. By William Markham Morton. (In preparation.)

of sand grains. We have not observed the male in the process of nest-building.

As stated in the literature the male, having constructed the nest, induces one or more females to enter it and lay eggs which he immediately fertilizes. He then maintains a guard over the eggs and newly hatched young, and perhaps provides aeration by his swimming or fanning movements.

In Karluk Lake many stickleback eggs have been found more or less scattered through aquatic vegetation. Possibly these eggs were deposited free, without construction of nests.

At Bare Lake, in 1955, C. W. Huver stripped eggs from female sticklebacks, fertilized them with macerated testes from mature males, and succeeded in hatching them in a bowl floated in a tub. At a water temperature varying from 9° to 16° C., the eggs were eyed in 9 days and started hatching at 14 days.

The embryological development of the threespine stickleback has been studied by Vrat (1949), who published a series of drawings of various stages. The development follows a pattern typical in teleost fishes.

Physiology and Behavior

The literature, at least in North America, contains little information regarding physiological responses, tolerances, and adaptations of the three-spine stickleback. It is believed to be a hardy fish in many respects. For instance, it is known to survive over winter in shallow lakes in northern temperate and subarctic zones, where the chemical conditions become severe. Dissolved oxygen sinks to a trace, and dissolved carbon dioxide and other gases build up considerable tensions. The mechanism for survival is not known; presumably it combines a greatly reduced metabolic rate with the ability to extract oxygen at low pressure.

The threespine stickleback has been used, particularly in Europe, as an aquarium fish. Possibly it would be a satisfactory subject for tank and jar experiments on physiological responses and adaptations. However, Cope et al. (1949) state that "Sticklebacks could not stand holding in the live jars, and mortalities were high at 24 hours." These authors used *Gasterosteus aculeatus* for some experiments in tolerance to certain insecticides. They found the stickleback t be more tolerant to emulsions of DDT, benzen hexachloride, chlorinated camphene, and chlorda than were salmonid fishes (the criterion of tole ance being the amount of agitation after 15-mi ute test periods). However, in certain tests wit acetone solutions of pyrethins they noted tha the sticklebacks "were rendered helpless withi the time of treatment, while only a few salmonid were so affected." They suggest that selectiv poisoning might possibly be used in control o sticklebacks. Jones (1935, 1938, 1939, 1947) ha made extensive use of *Gasterosteus aculeatus* a a test fish, particularly in determining the tox icity of various metals to fish.

The sticklebacks in Karluk and Bare Lake apparently suffer a heavy mortality after spawn ing. The physiology of this post-spawning mor tality is not known. Feeding apparently con tinues until the time of spawning but perhap ceases with spawning. The dead, spawned-ou fish picked up along shores are extremely ema ciated.

Except for spawned-out fish, nutrition is satis factory. All individuals are in reasonably plum condition throughout the summer. Nothing known concerning diseases in the Karluk an Bare Lake sticklebacks.

These fish harbor various parasites. One o these is the ligulid cestode, *Schistocephalus*, th plerocercoids of which lie in the abdominal cav ity of the fish. Crustacea are the host of th initial larval stage, and fish-eating birds, such a mergansers, of the adult tapeworm. At leas 20 percent of the adult sticklebacks are infested These cestode larvae reach 20 mm. or more i length, and one larva can fill all the availabl space in the fish and cause a visible distensio of the abdomen. A few of the infested fish hav from 2 to 8 of the worms each.

Morton (1942) states that the stickleback i Karluk Lake carries in its intestines the larv of a proteocephalid cestode, presumably *Proteo cephalus arcticus* Cooper. The adult worm found in the intestine of the lake charr, *Salvelinu alpinus*, which feeds on the stickleback.

Also reported by Morton, a larval cestode o the Dyphyllobothriid type, provisionally calle *Dibothrium fasteni*, is found in the stickleba as well as in the lake charr and in young re

mon. It occurs either free or in a cyst on the cera. Presumably it is the worm, the adult m of which has been reported from bears and rgansers as *Diphyllobothrium.*

A nematode, identified by Morton [4] as *Dacnitis vis* Zschokke and Heitz, is fairly common in stomach and intestine of the stickleback, ually occurring in small numbers. This worm found in both species of charr (*Salvelinus pinus* and *S. malma*). Morton reports also an nthocephalan worm, *Neoechinorhynchus rutili* üller), in the Karluk Lake stickleback and tes that Meyer (1932) has found this worm in cklebacks (*Gasterosteus*) in Europe.

A parasitic copepod, identified by Wilbur M. id as *Ergasilus cotti* Kellicott, is found on the rluk Lake sticklebacks. A large proportion of fish carry from 1 to 5 of these copepods each, ached to the skin at the base of the pelvic or rsal fins or more often in the gill chamber and ls.

Bigelow and Schroeder (1953) state that the ckleback "is a proverbially pugnacious fish, ng its spines with good effect as weapons of ense and defense, even on fishes much larger an itself." We have not observed any demonration of this pugnacity in the sticklebacks in rluk and Bare Lakes. As will be discussed der food habits, the stickleback in these waters not known to feed on other fishes large or small. is preyed upon by the arctic charr, but the act capturing a stickleback by a charr has not been served. We may surmise that the act takes so tle time that the stickleback has no opportunity r defensive action. Juvenile red salmon have en found with sticklebacks in their mouths or omachs, but the act of capture has not been served.

According to our observation, the stickleback pends to a large extent for protection on a rt of camouflage. In clear, calm water, over shoal, it will lie at the surface, perfectly moless for many minutes at a time. In such position, it resembles a floating stick or twig. It is possible that the male stickleback makes fective use of his spines in chasing females to the nest and in guarding the nest after the gs are laid.

[4] See footnote 2, p. 543.

Food Habits

Norman (1936), Jordan (1905), and others have remarked on the voracity of *Gasterosteus aculeatus* and stated that it is strongly predaceous on the eggs and young of other fishes. However, Markley (1940) found the sticklebacks of Sacramento River (sample taken in October) to be feeding mainly on insects and other invertebrates, especially amphipods. Carl (1953) examined a small number of stickleback stomachs from Cowichan Lake, British Columbia, and found zooplankton (Cladocera, copepods, amphipods) and insect larvae to be the chief items in the diet. Bigelow and Schroeder (1953) list as food for the threespine stickleback in the Gulf of Maine copepods, isopods, small shrimp, young squid, diatoms, small fish fry, and fish eggs. It is evident that the stickleback will eat a wide variety of (animal) foods depending on what is available.

Stomach examinations of sticklebacks in Karluk and Bare Lakes are summarized in tables 8–10. The larvae and pupae of chironomid flies (Diptera) were found, often in considerable numbers, in a large percentage of the stomachs. Other insects, such as caddis-fly larvae and damselfly and stonefly nymphs, occurred irregularly.

Also of importance were copepods, of the genera *Diaptomus* and *Cyclops;* and Cladocera, of the genera *Daphnia* and *Bosmina.* Stomachs were examined that contained well over 200 invertebrate plankters of 1 one more of these 4 genera.

TABLE 8.—*Contents of stickleback stomachs, Bare Lake, 1951*

[Numbers in parentheses are range of number of organisms per stomach]

Food	Date					
	June 13	June 29	July 8	Aug. 7	Sept. 12	Totals
Number of stomachs containing food	15	14	17	17	16	79
Number of stomachs containing—						
Chironomids	14 (4–124)	9 (5–88)	11 (1–11)	9 (1–104)	2 (2–3)	45
Other insects	7	8	5	13	5	38
Copepods	14 (7–63)	10 (2–36)	16 (1–16)	10 (1–108)	16 (7–242)	66
Cladocera	2 (1–2)	3 (1–5)	15 (1–112)	9 (2–218)	13 (11–229)	42
Ostracods	3 (1–2)	3 (1–2)	5 (1–11)	1 (1)	6 (1–121)	18
Rotifers	1 (1)		9 (2–15)			10
Clams	1 (9)	1 (1)		1 (5)	3 (1–7)	6
Stickleback eggs	4 (1–3)	2 (1–11)				6

TABLE 9.—*Contents of stickleback stomachs, Karluk Lake*

[Numbers in parentheses are range of number of organisms per stomach]

Food	Date							
	June 4, 1948	June 7, 1948	June 13, 1948	July 25, 1948	July 7, 1949	Aug. 9, 1949	Sept. 13, 1949	Totals
Number of stomachs containing food	11	23	50	15	68	25	25	
Number of stomachs containing—								
Chironomids	7 (4–14)	10	9		31	2	3	
Other insects	1				4			
Copepods	10 (11–20)	23	22	9 (1–71)	59 (1–276)	24	25	
Cladocera	3	20		13 (1–182)	31	23	25	
Ostracods	3 (1)	2	2	5 (1–22)	9 (1–134)	1	1	
Rotifers	2	13	24		1	1		
Clams					2			
Stickleback eggs		1		5 (1–38)	23 (5–58)	1		

TABLE 10.—*Contents of stickleback stomachs from fish of three size groups, Karluk Lake, July 7, 1949*

Food	Standard length of fish, mm.		
	31–45	46–60	61–75
Number of stomachs containing food	21	23	24
Number of stomachs containing—			
Chironomids	11	10	10
Other insects		1	3
Copepods	20	19	20
Cladocera	14	14	3
Ostracods	1	2	6
Rotifers		1	
Clams		2	
Stickleback eggs		3	20

Ostracods and rotifers were present. Several stomachs contained pea clams, sometimes in large enough numbers to constitute considerable bulk. Other food items, encountered only occasionally, included snails, leaches, planarians, and water mites. Vegetation or phytoplankton, in identifiable form, was never or scarcely ever present.

Several stomachs contained fish eggs, easily identifiable as stickleback eggs. No other fish material was found.

Some changes in the feeding habits throughout the summer may be noticed (tables 8 and 9). Chironomids were fewer in the stomachs in the latter part of the season. Various plankton invertebrate species fluctuated in numbers in the stickleback diet, probably in relation to fluctuations of numbers of these species present in the water.

There are also differences in the food selected by fish of various size groups (table 10). Fewer of the large fish were feeding on Cladocera, more of them on ostracods. Stickleback eggs were found in only the larger fish. Possibly the eggs are too large to be swallowed by the small fis Or perhaps the larger fish were in a nesting ar and thus had ready access to eggs.

Role as Prey

Several species of fish present in Karluk ar Bare Lakes may be predators on the stickleba The arctic charr (*Salvelinus alpinus*), which do not occur in Bare Lake, is a year-round reside in Karluk Lake in substantial numbers. Accor ing to Morton [5] and DeLacy [6], this charr fee on sticklebacks and stickleback eggs, especially the months of June and July. In the study the food habits of the arctic charr, in the Wo River drainage in western Alaska, it was fou that the charr consumed large numbers of stickl backs, particularly when young red salmon we not readily available.

The Dolly Varden charr (*Salvelinus malma*) said by Morton not to utilize sticklebacks in Ka luk Lake. Of 60 stomachs of Dolly Varden tak in Bare Lake in the period June–August 19 only 3 contained stickleback. It is likely th sticklebacks are eaten to some extent by t fingerling coho salmon and the rainbow tro especially during the winter, when food ite such as insects are not available in large numbe Baxter (1956) found the stickleback to be important item in the diet of the rainbow tro in a lake near Anchorage, Alaska. Also, t

[5] See footnote 2, p. 543.

[6] Contributions to the life histories of two Alaskan cha *Salvelinus malma* (*Walbaum*) and Salvelinus alpinus (Linnaeu By Allan Clark DeLacy. Doctoral thesis, University of Wa ington, Seattle. (Typewritten) 114 pp., 1941.

ulpin *Cottus aleuticus* may eat stickleback eggs d small sticklebacks.

Sticklebacks are eaten by several kinds of birds cluding probably mergansers (Munro and emens, 1937), gulls, loons, and kingfishers. ne quantitative relationships are not known. some significance to the overall ecology of the ke may be the fact that the stickleback carries e or more species of internal parasites which e transmitted to other fish or to birds.

The stickleback has been used to some extent northwestern Europe in the production of h oil and meal, and in Russia and possibly in rthwestern Alaska for human food. It has en reported that sticklebacks on Kodiak Island metimes are used for dog food, and are con-med by humans on occasion. For these uses e fish are stored in frozen blocks.

lation to Red Salmon

Aside from such intangible things as dual oc-pation of and competition for space, the rela-n between the stickleback and the production young red salmon involves four possible major ctors: the predation of the stickleback on the lmon, food competition between the stickleback d the young salmon, the use of stickleback fry eggs as food for the salmon, and the role of e stickleback in the diet of charr and other redators on the salmon.

Predatory habits of the stickleback have been entioned by various authors. Kincaid (1919) akes the (unsupported) statement: "The dam-e done by the stickleback is out of proportion his size, as he is able to kill the fry of larger h, notably the salmon, for which reason the ckleback is known locally as the Salmon iller." We have no evidence of sticklebacks in arluk and Bare Lakes feeding on red salmon gs or fry. We have not examined any stickle-ck stomachs taken in the spring while the lmon fry were very small. Rounsefell (1958), ates that: "there seems to be little evidence a they [sticklebacks] are actual predators (on ung salmon)." Rounsefell cites White (1930) ho performed experiments on the consumption brook trout (*Salvelinus fontinalis*) fry by rge trout of the same species and by adult reespine sticklebacks. The results of White's periments showed the stickleback to be an al-most negligible factor in the loss of trout fry. Rounsefell comments, "Salmon fry are much larger than the fry of the brook trout, so that there would seem to be even less chance of any destruction."

The feeding habits of the young red salmon in Karluk Lake are not fully known. It is probable that the fry eat insects and plankton animals, but the larger juveniles may eat a few small fish. Therefore, although there may be some points of difference, the food habits of the small red salmon and the sticklebacks are similar in large measure. Both fishes eat insect larvae (mainly chironomids) and plankton crustaceans. The diet is suited to the fare. Whether and to what extent the consumption of part of the available food supply by the stickleback has an adverse effect on red salmon production is not a matter easy to assess.

As we have suggested above, small sticklebacks may be an item in the food supply of the salmon fingerlings, especially the larger smolts. However, data for making a quantitative estimate of the effect on salmon production are lacking.

Certain predators, in particular the arctic charr, have been shown to utilize sticklebacks for food. This use of sticklebacks may in some measure relieve predation on the young red salmon and possibly be a favorable factor in the production of salmon smolts. However, relationships between predators and prey are complex and not understood fully. A reduction in numbers of sticklebacks present in Karluk Lake might mean that more salmon would be eaten by the charrs. Or it might mean only that the charr population would decline, because the total food supply had decreased, and thus the number of salmon smolts eaten by chars might remain substantially the same.

SUMMARY

The threespine stickleback, *Gasterosteus aculeatus*, is found in large numbers in Karluk Lake and Bare Lake in southwestern Kodiak Island, Alaska. Its presence may have a relation to the production of red salmon (*Oncorhynchus nerka*) in these waters.

This species of stickleback has a wide distribution in the subarctic and temperate zones of the northern hemisphere. It has had a history

of much confusion in classification and nomenclature, largely because of wide variations in morphological characters from one locality or one type of environment to another. The stickleback in Karluk and Bare Lakes is of the partially naked (few lateral plates) form, which is characteristic of populations that reside permanently in fresh water. Counts of lateral plates and fin rays show the populations of the two lakes to be discrete.

Estimates of numbers of fish in the stickleback populations are difficult to make. Sticklebacks appear to be more numerous in Karluk and Bare Lakes than any other species. There is evidence of considerable fluctuation in numbers from year to year.

The sticklebacks are often to be found in large numbers along the shoals and have been observed on the surface in the center of the lake and in small numbers in deep water. Apparently there is little or no movement to and from the ocean, but spawning runs ascend the two main tributaries of Karluk Lake to Thumb and O'Malley Lakes.

The species is at least moderately hardy and resistant to adverse conditions. It carries several species of parasites in these waters, notably the pleroceroid of a cestode (*Schistocephalus*) which has a plankton crustacean (Cladocera) as its initial host and a bird as the final host.

The sexually mature fish have both male and female gonads. The male has paired ovaries and the female a mass of testicular tissue. A large female from Karluk Lake had several eyed eggs in the ovary.

Spawning takes place in early summer. In some years a part of the spawning occurs as late as August. In these waters the male does not use plant material to any great extent in constructing the nest (as has often been reported in the literature), but makes a nest of sand cemented together with a secretion from within his body and more or less buried in sand and gravel in shoal water. Sticklebacks may spawn also in weed beds, with little or no nest construction.

The lifespan is about two and one-fourth years. A standard length of 60 to 65 mm. is attained in Bare Lake and up to 80 mm. in Karluk Lake. Spawning may occur only once during life or at most twice. At least part of the fish d within a few weeks after spawning.

The principal foods for the stickleback in bot lakes are midge fly (Chironomid) larvae, ar plankton crustacea (Copepods, Cladocera, Ostr coda). Minor items include other insects, wat mites, rotifers, small clams, snails, leeches, ar stickleback eggs. Stomachs examined at variou times during the summer did not contain egg or fry of fish other than sticklebacks. The perio covered by these examinations included th spawning time of the red salmon, but not th time of emergence of red salmon fry.

The stickleback is a component of the food o the arctic charr, which is a predator also on youn red salmon. Birds, rainbow trout, and possibl large juvenile coho salmon eat stickleback Small sticklebacks may be used to a small exte as food by the larger juvenile red salmon.

The principal means by which the sticklebac in Karluk and Bare Lakes may influence re salmon production include competition wit young salmon for food and by reducing predato pressure on red salmon by furnishing food to th charr. Quantitative information is insufficient t assess accurately the benefit or harm to salmo production caused by the stickleback populatio

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